Reduction of *Schizostylis* (Iridaceae: Ixioideae) in *Hesperantha*

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ABSTRACT. *Schizostylis* has the floral synapomorphies of the African genus *Hesperantha*, including style branches dividing at the mouth of the floral tube, long laxly spreading style branches, and articulated anthers twisted to face inward. The basic chromosome number of *Schizostylis*, $x = 13$, is shared in Ixioideae by *Hesperantha*, *Geissorhiza*, and a few species of *Romulea*. *Schizostylis* then differs from *Hesperantha* only in its red flowers (occasionally pink) and, more importantly, in its rootstock, a short rhizome. Most species of *Hesperantha* have white or pink flowers, occasionally yellow or purple, and all have corms with hard woody tunics. We suggest that *Schizostylis*, which is semi-aquatic and grows along streams in seasonally or permanently waterlogged ground, has acquired a rhizome secondarily by loss of the corm. Neither the rhizome nor the red flower is sufficient grounds to warrant generic separation from *Hesperantha*.

Schizostylis, a monotypic, or at best ditypic, genus of southern African Iridaceae subfamily Ixioideae, extends from the Drakensberg Escarpment of Eastern Cape Province, South Africa, northward through Lesotho, Swaziland, and Mpumalanga Province to eastern Zimbabwe. A plant of habitats that are waterlogged during its spring and summer growing season, *Schizostylis* grows along streams, wet seeps, and the edges of marshes (Goldblatt, 1991, 1993). Except in its rhizomatous rootstock and red (sometimes pink) flowers, *Schizostylis* closely resembles the large African genus *Hesperantha* (ca. 65 spp.) morphologically, and it has all of the critical floral features of that genus. These include green, soft-textured bracts; a well-developed perianth tube; a style dividing at the top of the perianth tube; long, spreading filiform style branches; and anthers twisted to face inward. The last three features are synapomorphies for *Hesperantha*. *Schizostylis* also shares a derived basic chromosome number, $x = 13$, with *Hesperantha*, *Geissorhiza*, and some species of *Romulea* (Goldblatt, 1971). Here we address the hypothesis that *Schizostylis* is not only immediately related to *Hesperantha* but is also closely related to species within that genus, thus nested in *Hesperantha*.

ROOTSTOCK

The primitive or plesiomorphic rootstock for all genera of subfamily Ixioideae (Goldblatt, 1990, 1991) is a corm that produces roots from below. A corm is considered one of several synapomorphies for this large subfamily of ca. 27 genera and 950 species. Solely because of its rhizomatous rootstock, *Schizostylis* was treated by Hutchinson (1934) as a member of tribe Aristeae (subfamily Nivenioideae sensu Goldblatt, 1990) despite its many morphological features being discordant with that tribe. *Schizostylis* has all the derived features of Ixioideae. These include flowers with a well-developed perianth tube, perianth lasting more than one day, and flowers sessile and subtended by two opposed floral bracts (inflorescence usually a spike). In their internal anatomy, the leaves of *Schizostylis* also accord with Ixioideae, having epidermal cells with sinuous margins and multiple papillae, and mesophyll cells elongated at right angles to the axis (Rudall & Goldblatt, 1991). In addition, *Schizostylis* has pollen grains typical of Ixioideae with perforate exine and a two-banded operculum, synapomorphies for Ixioideae (Goldblatt et al., 1991). There can be no doubt, then, that *Schizostylis* is a member of subfamily Ixioideae and that its floral specializations point to a close relationship with *Hesperantha*.

Similar rhizome-like rootstocks are known in a few other species of Ixioideae. These include *Gladiolus sempervirens* G. Lewis and *G. aquamontanus* Goldblatt & Vlok, both derived species of this large genus that grow in permanently moist habitats (Lewis et al., 1972; Goldblatt & Vlok, 1989). Likewise, some species of *Geissorhiza* that grow in wet habitats, e.g., *G. outeniquensis* Goldblatt, *G. cataractarum* Goldblatt (Goldblatt, 1985), *G. uliginosa*

Goldblatt & J. C. Manning (Goldblatt & Manning, 1995), have corm tunics more or less membranous and the corms much reduced in size and very different from those of species from more conventional habitats. We suggest that the rhizome or reduced corms of these species are simply a habitat adaptation. Corms are primarily adapted for underground survival during a long dry season and short growing season and hence not suited to plants that grow in permanently wet sites. The rhizome of *Schizostylis* thus appears to be a secondary specialization, as suggested by Goldblatt (1971, 1991), associated with its aquatic habitat. The presence of corm-like axillary propagules on the stems of at least some *Schizostylis* plants strengthens the hypothesis that the rhizome is secondary in the genus. No member of any subfamily of Iridaceae produces axillary cormlets excepting those that have a cormous rootstock.

The *Schizostylis* Flower

Although the flower of *Schizostylis* conforms in all its critical features to that of *Hesperantha*, it differs from all species of that genus (Goldblatt, 1984; Hilliard & Burtt, 1986) in its bright red color. It is also somewhat unusual in having a particularly long perianth tube, ca. 25–35 mm long. Several species of *Hesperantha* in eastern southern Africa, for example, *H. grandiflora* G. J. Lewis, *H. huttonii* (Baker) Hilliard & Burtt, *H. pulchra* Baker, and *H. scopulosa* Hilliard & Burtt, have comparably long or even longer tubes, but they all have pink flowers. Red flower color combined with a long perianth tube, prominent anthers, and a flowering season from mid to late summer are often associated with a specialized pollination syndrome (Johnson & Bond, 1994) using exclusively the butterfly *Aeropetes* (*Meneris*) *tulbaghia*. *Schizostylis* may be a member of this pollination guild although there are no published observations on the pollination of *S. coccinea*. Flowers of *Schizostylis* are thus no reason to exclude the genus from *Hesperantha*. Both the elongate perianth tube and the red flower color are almost certainly adaptations to a particular pollination system, and are not evidence of a fundamentally different ancestry.

Discussion

Although a critical phylogenetic analysis of *Hesperantha* or of its allies is not available, it seems beyond reasonable doubt that there is no sound taxonomic reason to continue to recognize *Schizostylis* as a separate genus. It is almost certainly most closely allied to long-tubed, eastern southern African species of *Hesperantha*. Its distinguishing features, the rhizome and a long-tubed red flower are adaptations to a wet habitat and a particular pollinator, respectively. Neither feature is unique in Ixioideae. A rhizome-like rootstock or highly reduced corms are known in at least two other genera of the subfamily, in both of which they occur only in specialized species growing in perennially moist habitats. A specialized long- and narrow-tubed red flower is likewise found in a handful of species of other genera of the subfamily and, at least in some of these, e.g., *Gladiolus cardinalis* Curtis, *G. stephaniae* Obermeyer, *Tritoniopsis burchellii* (N. E. Brown) Goldblatt, *T. triticea* (Burman f.) Goldblatt, is known to be an adaptation for pollination by a particular insect, the butterfly *Aeropetes tulbaghia* (Johnson & Bond, 1994). Neither the loss of a corm and the reversion of the rootstock to a rhizome, nor an adaptation to a particular pollinator are alone sufficient grounds for recognition of a genus. This is particularly the case for a monotypic (or possibly ditypic) genus such as *Schizostylis* where its relationships can be confidently determined. We therefore propose reducing *Schizostylis* to synonymy in *Hesperantha*.

Hesperantha Ker Gawler, Konig & Sims Ann. Bot. 1: 224. 1805. TYPE: *Hesperantha falcata* (L.f.) Ker Gawler.

Schizostylis Backhouse & Harvey, Curtis's Bot. Mag. 90: pl. 5422. 1864. Syn. nov. TYPE: *Schizostylis coccinea* Backhouse & Harvey (= *Hesperantha coccinea* (Backhouse & Harvey) Goldblatt & J. C. Manning).

Hesperantha coccinea (Backhouse & Harvey) Goldblatt & J. C. Manning, comb. nov. Basionym: *Schizostylis coccinea* Backhouse & Harvey, Curtis's Bot. Mag. 90: pl. 5422. 1864. TYPE: South Africa. Eastern Cape: without precise locality or collector, cultivated in Britain, illustration in Curtis's Bot. Mag. 90: pl. 5422 (1864).

Schizostylis pauciflora Klatt (1867) appears to be no more than a pink-flowered form of *S. coccinea*, although both were recognized by Baker (1896). The two were treated as conspecific by Goldblatt (1993) and we endorse this treatment. Pink-flowered plants at least sometimes grow among those with red flowers and they have been recorded at several sites within the range of typical red-flowered *S. coccinea*. Thus, there is no geographical component to the distribution of the two flower colors in the species.

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